Behavioral plasticity and the valence of indirect interactions

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Behavioral plasticity in animals often transforms direct interactions between species, but its effects can spread through ecological networks in unexpected ways, creating indirect interactions that are difficult to predict. We present a theoretical framework to understand how species-level behavioral changes influence these indirect interactions and the overall dynamics of ecological networks. As an illustrative example, we analyze predators that feed on two types of prey, each of which temporarily transitions into a state of reduced activity and growth after evading an attack, to decrease vulnerability. Coarse-grained models show that this hiding behavior can shift the indirect interaction between prey species from apparent competition to mutualism or parasitism. These shifts occur when the predator's capture efficiency falls below a threshold, causing frequent hunting failures. This inefficiency leads to one prey species indirectly protecting the other by drawing predator attention, paradoxically increasing predator biomass due to reduced hunting success. Interestingly, empirical capture probabilities align with the range where such shifts are predicted. We describe these changes in the qualitative nature of species interactions as shifts in "interaction valence," emphasizing how routine animal behaviors can generate indirect effects that defy intuition and reshape community structure through cascading effects across the network.

Keywords: predator-prey | coarse-graining | competition | mutualism

Introduction

Instances where seemingly entrenched interactions between species abruptly change have now been observed in most ecosystems and across taxa. Included are shifts from competition to facilitation among terrestrial plants in harsh environments (Bertness & Callaway 1994) or among bacteria in biofilms (Nadell *et al.* 2016); dynamic shifts between competition and predation (Fahimipour & Anderson 2015), competition and cooperation (M. A. Gil & Hein 2017), or parasitism and mutualism in fishes (Bshary *et al.* 2008); the induction of cannibalism among competing protozoans (Giese 1938), rotifers (Gilbert 1973), and amphibians (Collins &

Cheek 1983); or even reversals of predator and prey identity among marine invertebrates (Barkai & McQuaid 1988).

These examples emphasize how changes in the behavior or physiology of interacting organisms can alter the valence of their interactions (Huang & Sih 1990; Winnie Jr 2012; Fahimipour & Anderson 2015; M. Gil *et al.* 2019; Gaiarsa *et al.* 2021). Such shifts can significantly impact ecosystem dynamics (Neutel *et al.* 2007) through indirect effects that propagate through ecological networks (Dunne & Williams 2009; Fahimipour, Anderson & Williams 2017). For instance, predators not only reduce prey numbers through consumption but also induce behavioral changes that affect prey demographics and interactions with other species (Schmitz, Beckerman, *et al.* 1997; Schmitz, Krivan, *et al.* 2004). This is evident in behaviorally mediated trophic cascades (Schmitz, Beckerman, *et al.* 1997; Schmitz, Krivan, *et al.* 2004), where prey's fear of depredation increases biomass in lower trophic levels (Abrams *et al.* 1996; Beckerman *et al.* 1997; Schmitz, Beckerman, *et al.* 1997; Schmitz & Suttle 2001; Schmitz, Krivan, *et al.* 2004). However, our understanding of how behavior influences other indirect effects, including inherently indirect interactions like apparent competition (Holt 1977; Holt & Bonsall 2017; Schreiber & Křivan 2020), remains less developed (Schreiber, Bürger, *et al.* 2011).

Here, we present a theoretical framework for understanding how behavioral plasticity influences indirect interactions within ecological networks. Our approach leverages the natural time scale separation between behavior and demography (Holling 1959; O'Dwyer 2018; Hein & Martin 2020) and employs methods for quantifying indirect effects using properties of the system Jacobian matrix (Bender *et al.* 1984; Yodzis 2000; Aufderheide *et al.* 2013; Novak *et al.* 2016). We apply the method to a common ecological motif: a predator feeding on two prey species that do not directly compete with one another, known as apparent competition (Holt 1977; Holt & Bonsall 2017; Schreiber & Křivan 2020). To illustrate the method, we examine how a widespread animal behavior — hiding, wherein prey respond to predator encounters by entering a temporary state of reduced vulnerability and foraging success (Sih 1987) — alters the direction of indirect effects between apparent competitors. Depending on prey behavioral parameters and the predator's hunting performance, we find that hiding prey can inhibit each other's population growth, as seen in classic apparent competition; exhibit an apparent parasitism-like relationship, where one prey benefits from the other's increased density while the other is harmed; or form an apparent mutualism, where both prey benefit from each other's increased abundance. Our method demonstrates how qualitative variability in indirect interactions, which we term *interaction valence*, can be discovered and characterized within ecological networks.

Methods

The apparent competition motif consists of two prey species that are consumed by a shared predator (Holt 1977). Suppose that we divide both prey species $k \in [1, 2]$ into two subpopulations each: the "foragers" (denoted as F_k), actively foraging in the local habitat, and the "hiders" (denoted as H_k), which have entered a state of

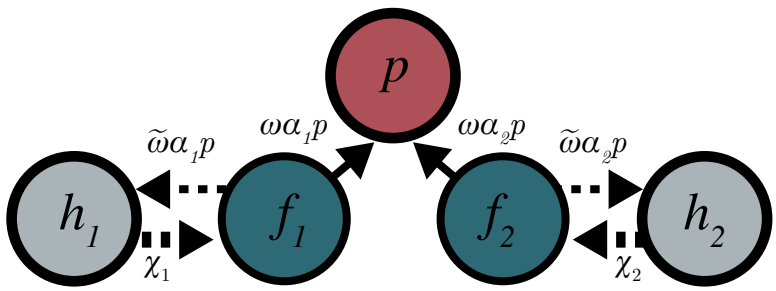

Figure 1: **Full system before model reduction.** The network illustrates the primary biomass flows within the system. Solid arrows denote trophic links between predator and prey, while dashed lines represent biomass flows due to behavioral state transitions (*i.e.*, individuals switching from foraging to hiding and back). The *per capita* rates of each reaction are indicated, with parameters described in Eq. 2. To ensure that hiding dynamics are fast, our model demands larger values of χ_k relative to the new normalized time units ($1 \ll \chi_k$). The reduced model (Eq. 5) is derived from the set of processes depicted here.

reduced activity following a failed predation attempt (Fig. 1). Assuming encounters between both prey species and the predator are governed by mass-action, we have

$$\dot{F}_k = r_k F_k \left(1 - \frac{F_k}{K_k}\right) + x_k H_k - a_k F_k P \tag{1a}$$

$$\dot{H}_k = \tilde{\omega} a_k F_k P - x_k H_k \tag{1b}$$

$$\dot{P} = \omega \sum_k e_k a_k F_k P - mP. \tag{1c}$$

Here, F_k are foraging prey; H_k are prey that are hiding; and P is a shared top predator. The parameters r_k are prey growth rates (t^{-1}); K_k are prey carrying capacities (individuals $\cdot$ area^{-1}); x_k are rates at which hiding prey resume foraging (t^{-1}); a_k are attack rates of predators on prey (area $\cdot$ predator^{-1} $\cdot$ t^{-1}); ω and $\tilde{\omega}$ are predator probabilities of attack capture success and failure respectively, with $1 = \omega + \tilde{\omega}$; e_k are trophic efficiencies (predator $\cdot$ prey^{-1}); and m is the predator mortality rate (t^{-1}). We assume: [*i*] hiding prey are temporarily invulnerable but they also acquire fewer resources and hence their growth is negligible, [*ii*] prey that escape predators always hide, and [*iii*] hiding does not involve competition for resources such as finite shelters, so arbitrary numbers of prey can hide at once.

Nondimensionalization

Before proceeding, the number of model parameters can first be reduced by transforming variables and parameters into nondimensional quantities (Gurney & Nisbet 1998; Hastings & L. J. Gross 2012). The result is a model in which we have rescaled rates by the mean generation time of top predator individuals (m^{-1}). Making the following substitutions:

$$f_k = \frac{F_k}{K_k},\ h_k = \frac{H_k}{K_k},\ p = \frac{P}{e_1 K_1},\ \rho_k = \frac{r_k}{m},\ \alpha_k = \frac{a_k K_1 e_1}{m},\ \chi_k = \frac{x_k}{m},\ \eta = \frac{e_2 K_2}{e_1 K_1},\ \tau = tm$$

we have the nondimensionalized system of equations (Fig. 1)

$$\dot{f}_1 = \rho_1 f_1 (1 - f_1) + \chi_1 h_1 - \alpha_1 f_1 p \tag{2a}$$
$$\dot{h}_1 = \tilde{\omega}\alpha_1 f_1 p - \chi_1 h_1 \tag{2b}$$
$$\dot{f}_2 = \rho_2 f_2 (1 - f_2) + \chi_2 h_2 - \alpha_2 f_2 p \tag{2c}$$
$$\dot{h}_2 = \tilde{\omega}\alpha_2 f_2 p - \chi_2 h_2 \tag{2d}$$
$$\dot{p} = \omega p (\alpha_1 f_1 + \eta\alpha_2 f_2) - p \tag{2e}$$

where the derivatives are with respect to our new units of time.

Time scale separation

We assume that prey behavioral transitions are fast compared to prey population demographics (at least approximately), and that both of these processes are faster than predator mortality, implying $1 < \rho_k < \chi_k$. This allows us to reduce the system using a separation of time scales. For total prey biomass $n_k = f_k + h_k$, we make the substitution $f_k = n_k - h_k$ and differentiate to obtain the slow dynamics

$$\dot{n}_1 = \dot{f}_1 + \dot{h}_1 = \rho_1(n_1 - h_1)\left[1 - (n_1 - h_1)\right] - \omega\alpha_1(n_1 - h_1)p \tag{3a}$$
$$\dot{n}_2 = \dot{f}_2 + \dot{h}_2 = \rho_2(n_2 - h_2)\left[1 - (n_2 - h_2)\right] - \omega\alpha_2(n_2 - h_2)p \tag{3b}$$
$$\dot{p} = \omega p\left[\alpha_1(n_1 - h_1) + \eta\alpha_2(n_2 - h_2)\right] - p. \tag{3c}$$

We now consider the fast dynamics of h_k. Assuming these fast variables quickly reach their steady state values $h_k^\star$, we set $\dot{h}_k(h_k^\star) = 0$ (Eq. 2) to find $h_k^\star$:

$$h_k^\star = \frac{\tilde{\omega}\alpha_k n_k p}{\chi_k + \tilde{\omega}\alpha_k p}. \tag{4}$$

Substituting the steady state densities of hiding individuals $h_k^\star$ back into the equations for $\dot{n}_k$, and $\dot{p}$ (Eq. 3), we obtain the final reduced system (Table 1)

$$\dot{n}_1 = \rho_1\chi_1 n_1\phi_1(n_1, p) - \omega\frac{\alpha_1\chi_1 n_1 p}{\chi_1 + \tilde{\omega}\alpha_1 p} \tag{5a}$$
$$\dot{n}_2 = \rho_2\chi_2 n_2\phi_2(n_2, p) - \omega\frac{\alpha_2\chi_2 n_2 p}{\chi_2 + \tilde{\omega}\alpha_2 p} \tag{5b}$$
$$\dot{p} = \omega\left(\frac{\alpha_1\chi_1 n_1 p}{\chi_1 + \tilde{\omega}\alpha_1 p} + \eta\frac{\alpha_2\chi_2 n_2 p}{\chi_2 + \tilde{\omega}\alpha_2 p}\right) - p. \tag{5c}$$

We refer to the normalized rate at which hiding prey resume foraging, χ_k, as species "boldness" since higher values of this parameter indicate quicker returns to foraging after successfully escaping a predator attack. The function $\phi_k(n_k, p)$ is

$$\phi_k(n_k, p) = \frac{\chi_k(1 - n_k) + \tilde{\omega}\alpha_k p}{(\chi_k + \tilde{\omega}\alpha_k p)^2}, \tag{6a}$$

which defines density dependence and the effects of hiding on prey population growth, representing three processes. For prey spp. k, in addition to classical self-regulation, $\chi_k(1 - n_k)$, the growth function $\phi_k(n_k, p)$ captures the dual nature of

hiding in our model. Predator-induced hiding provides temporary invulnerability for prey individuals, reducing population mortality and enhancing growth ($\tilde{\omega}\alpha_k p$), but it also causes lost foraging opportunities, leading to factors $1/(\chi_k + \tilde{\omega}\alpha_k p)^2$. This balance between linear growth-enhancing and quadratic growth-suppressing effects of hiding (and hence, predator densities, which drive prey hiding behavior) is crucial in shaping the interaction dynamics. We note that the model reduces to standard apparent competition with logistic prey growth and type-I functional responses when predators are perfectly efficient hunters, $\omega = 1$; $\tilde{\omega} = 0$. In this case, hiding is never induced and so its effects on population demographics are not realized.

Analysis of prey interactions

The local stability of steady states $\mathbf{x}^\star = [n_1^\star, n_2^\star, p^\star]$ can be computed from linearizations of the dynamics, captured by the Jacobian matrix $\mathbf{J}$, which has entries

$$J_{ij} = \left.\frac{\partial \dot{x}_i}{\partial x_j}\right|_\star . \tag{7}$$

Our initial focus lies in understanding coexistence patterns and hence the location of transcritical bifurcations (Kuznetsov 1998) in the reduced model. We derive analytical test functions (T. Gross & Feudel 2004) to locate these bifurcations in parameter space, which occur when the determinant of the Jacobian matrix vanishes, $|\mathbf{J}| = \mathbf{0}$, marking the onset of a zero eigenvalue (Kuznetsov 1998).

Our second goal is to understand how the interaction between prey species changes with model parameters. To do this we quantify the net interaction between prey by accounting for direct and indirect effects through all paths in the motif (Bender *et al.* 1984; Nakajima 1992; Yodzis 2000; Aufderheide *et al.* 2013; Novak *et al.* 2016), which can be accessed directly from the Jacobian. To illustrate this, consider conceptually that we compute the steady state of the system as a function of parameters s, which we can write as $\mathbf{x}^\star = x^\star(s)$. Since we define our system as $\dot{\mathbf{x}} = g(\mathbf{x}, s)$ we know that $g(\mathbf{x}^\star(s), s) = 0$. Using a corollary to the implicit function theorem (Khalil 2002; Aufderheide *et al.* 2013) we can differentiate with respect to s to get

$$\frac{\partial g}{\partial \mathbf{x}}\frac{\partial \mathbf{x}}{\partial s} = -\frac{\partial g}{\partial s} \tag{8a}$$

$$\mathbf{J}\frac{\partial \mathbf{x}^\star}{\partial s} = -\frac{\partial g}{\partial s} \tag{8b}$$

$$\frac{\partial \mathbf{x}^\star}{\partial s} = -\mathbf{J}^{-1}\frac{\partial g}{\partial s}. \tag{8c}$$

Thus, the impact matrix that captures direct and indirect effects among species is $\mathbf{M} = -\mathbf{J}^{-1}$ (discussed in detail by Bender *et al.* 1984; Nakajima 1992; Yodzis 2000; Aufderheide *et al.* 2013; Novak *et al.* 2016), where the superscript indicates a matrix inverse. Because we are interested in apparent prey interactions, we focus analysis on entries $M_{1,2}$ and $M_{2,1}$, which permit a straightforward interaction classification: *apparent competition* occurs when both prey negatively impact one

another, $\max(M_{1,2},\ M_{2,1}) < 0$; *apparent parasitism* occurs when one prey benefits from the other while the other is negatively impacted, $\min(M_{1,2},\ M_{2,1}) < 0 < \max(M_{1,2},\ M_{2,1})$; and *apparent mutualism* occurs when both prey benefit from one another, $0 < \min(M_{1,2},\ M_{2,1})$. We note that this impact approximation is valid for small biomass perturbations, as Eq. 8 holds up to linear order.

To assess the tendency of the system to exhibit any of the possible indirect interaction modes outlined above, it is important to account for the effects of parameter variation in Eq. 5. By parameter variation, we mean the process of randomly drawing parameter values from biologically relevant distributions within the model (Eq. 5, Table 1), which can influence whether the system exhibits competition, parasitism, or mutualism as the type of apparent interaction. We quantify this tendency as the robustness, $\mathcal{R}$, of a given interaction type to variation in the parameter space of Eq. 5 (Lawton *et al.* 2024). Specifically, we define a binary variable $\Omega_q(s)$, which equals 1 if the n-dimensional vector of model parameters s corresponds to interaction type q, and 0 otherwise. The fraction of parameter space resulting in interaction type q is approximated over N random parameter set samples s_i (as detailed in Table 1):

$$\mathcal{R} = \frac{1}{N} \sum_i \Omega_q(s_i). \tag{9}$$

This approach allows us to approximate the size of the subregion of parameter space where the indirect prey interaction is of a specific type, providing a measure of how robust each interaction type is to variations in the model parameters. To assess the correlations between parameter values (Table 1) and the emergence of apparent mutualism, we employed a generalized linear model (GLM) with binomial error distribution and a logit link function. For each random parameter set, we defined a binary variable indicating the presence (1) or absence (0) of mutualism, determined as $\min(M_{1,2},\ M_{2,1}) > 0$. It is important to note that the GLM was used not to assess statistical significance, but to quantify correlations between the parameters and the probability of a mutualism emerging.

Results

We begin by analyzing model steady states, focusing on a scenario where the two prey species differ in their hiding strategy as defined by boldness, χ_k — the rate at which hiding individuals of sp. k resume foraging — but are otherwise

Parameter	Description	Range or Value
ρ_k	Intrinsic growth rate of prey sp. k	$[4, 25]$
η	Relative carrying capacity and reward potential of sp. 2	$[0.1, 4]$
χ_k	Foraging resumption rate ("boldness") of sp. k	$(1, 10) \times \rho_k$
α_k	Attack rate of predators on prey sp. k	$[0.5, 15]$
ω	Predator attack success probability	$(0, 1]$

Table 1: Parameter definitions and ranges used to compute model steady states and interaction robustness (Eq. 9; Fig. 3).

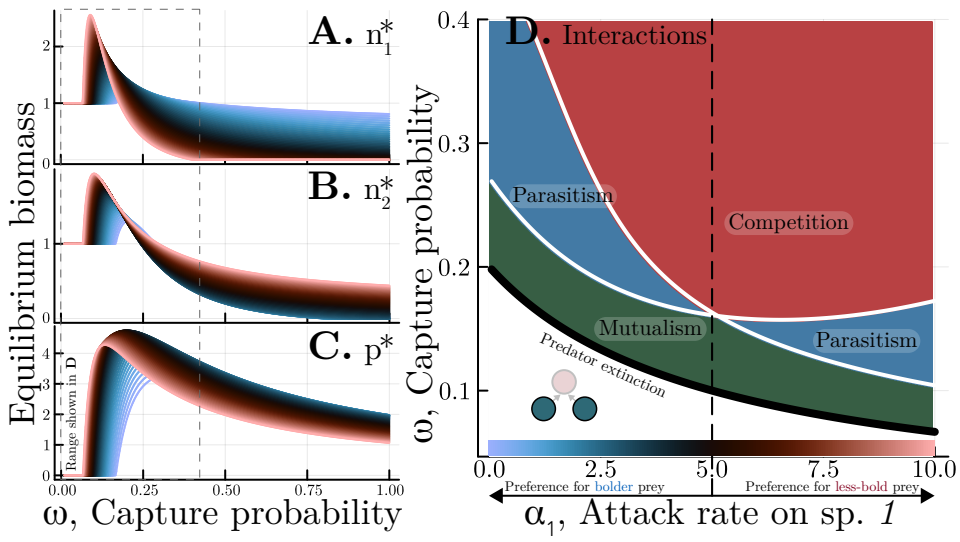

Figure 2: **Steady states and interaction modes. A.** Equilibrium biomass of prey species 1 ($n_1^\star$) as predator capture probability, ω (x-axis), and its attack rate on prey species 1, α_1 (colors), are varied. Color gradient indicates the predator's preference for either prey, with cooler colors representing a preference for the bolder prey species 2 ($\alpha_1 < \alpha_2$) and black representing equal preference ($\alpha_1 = \alpha_2$; colorbar shown on the x-axis of panel **D**). **B.** Equilibrium biomass of prey species 2 ($n_2^\star$) under varying ω and α_1. **C.** Equilibrium predator biomass ($p^\star$). Dashed gray box shows the range of ω values displayed along the y-axis of **D**. **D.** Interaction outcomes. The solid black bifurcation curve marks predator extinction. The apparent interaction between prey is competition, mutualism, or parasitism depending on α_1 and ω. Colors indicate valence: red for apparent competition, blue for parasitism, and green for mutualism. White curves delineate transitions between interaction modes, which occur when $M_{1,2} = 0$ and $M_{2,1} = 0$ (Eq. 8). Colorbar on the x-axis also corresponds to the surfaces in panels **A**–**C** (note that the blue in this color scale is unrelated to blue in **D**). Vertical line shows the attack rate on the bolder prey species 2 (α_2) for reference. Parameters are $\rho_k = 9.5$, $\alpha_2 = 5$, $\eta = 1$, $\chi_1 = 11$, $\chi_2 = 12$.

identical in terms of intrinsic growth rates ($\rho_1 = \rho_2$), carrying capacities, and reward potentials ($\eta = 1$). Under these conditions, we investigate the effects of changing predator preference for either prey (relative values of α_1 and α_2) and the capture success probability of predators, ω (see Eq. 5) on equilibrium biomass $\mathbf{x}^\star$. Most of the assumptions made here will be relaxed in the following section, where we present sensitivities of interaction patterns to parameter variation.

Steady states and interaction modes

Assume prey species 2 is bolder than species 1 ($\chi_1 < \chi_2$), meaning individuals of species 2 spend less time hiding after evading an attack on average. We consider two distinct cases. First, when $\alpha_1 > \alpha_2$, predators prefer the less-bold prey species 1. This could occur if some inherent preference for species 1 causes longer hiding times in that species as an adaptive response (*e.g.*, Holt & Bonsall 2017; Lima 1998). Alternatively, when $\alpha_1 < \alpha_2$, the predator prefers the bolder prey species 2. This might happen if the boldness of prey species 2 corresponds with some

other behaviors or characteristics that make them easier to encounter or detect (*e.g.*, Abrams 1984; Werner *et al.* 1983). This preference may also occur in cases where the predator encounters the bolder species more often, allowing it to develop better search images or attack strategies (Endler 1988).

Exploring the model steady states numerically, we find that interaction outcomes and biomasses depend strongly on predator capture probability ω and its relative preference for either the bolder ($\alpha_1 < \alpha_2$) or less-bold ($\alpha_1 > \alpha_2$) prey (Fig. 2A-C). Across a range of prey preferences, equilibrium biomass is maximized for all species, including predators, at *low* values of predator capture probability, ω, (Fig. 2A-C) near the transcritical bifurcation where predators are lost (Fig. 2D, black curve). This pattern holds across different preferences for either prey (*i.e.*, relative values of α_1 and α_2). This result is intuitive for prey species, which benefit from reduced top-down pressure as their shared predator becomes an inefficient hunter. However, it is surprising with respect to the predator species, which experiences fitness benefits as its attacks become less likely to succeed (Fig. 2C).

To understand the non-intuitive result of increasing predator biomass with decreasing hunting success, we analyzed the interaction between prey species. We found a sharp threshold in predator capture probability, ω, below which the interaction transitions from negative (*i.e.*, apparent competition) to positive (*i.e.*, apparent mutualism or parasitism; Fig. 2D), which explains why predator biomass is maximized near critical values of its own capture efficiency. This occurs because a reduction in hunting success functions to eliminate or reverse negative feedbacks between prey species, ultimately leading to long-term population benefits for the entire motif. Predator biomass is maximized near the point where the two white curves in Fig. 2D, describing vanishing impacts of each prey, intersect (compare Figs. 2C and 2D). Precisely at the intersection of these curves, prey species biomasses become completely decoupled from one another. Thus, near this point, predators are consuming two effectively independent resources engaged in an apparent neutrality. These results are summarized as interaction outcomes based on α_1 and ω values (Fig. 2D). The solid black bifurcation curve indicates predator extinction, while the regions of apparent competition, mutualism, and parasitism are denoted by red, green, and blue, respectively.

Robustness of apparent mutualism

The potential for apparent mutualism between prey to emerge depends on model parameters. Fig. 3A shows the correlations between parameter values and the probability that a random stable community described by Eq. 5 will exhibit apparent mutualism. Negative coefficients mean that larger values of that parameter reduce the chance of observing a mutualism. These correlations identify the parameters that most strongly influence interaction outcomes. Specifically, apparent mutualisms are most likely in communities with inefficient predators (small ω; Fig.2D; Fig.3), prey individuals that hide for longer periods (smaller χ_k), weaker top-down interactions (smaller α_k), faster intrinsic prey growth (larger ρ_k), and asymmetric prey reward potentials and carrying capacities (smaller η).

Given the outsized role of predator capture success, ω, in the emergence of

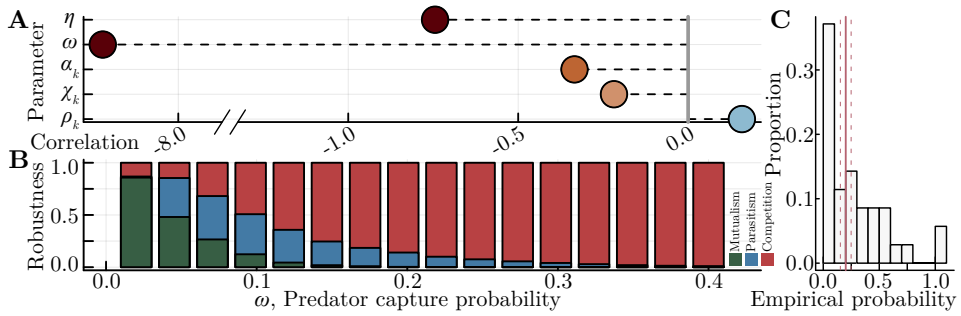

Figure 3: **Parameter sensitivities and robustness of interaction modes. A.** Correlation between parameter values and the emergence of apparent mutualisms. Negative coefficients indicate that smaller values of that parameter increase the probability that a random community described by Eq. 5 will exhibit apparent mutualism. Correlations estimated using a generalized linear model with binomial error distribution and a logit link function. Color gradient indicates the magnitude, with darker colors representing stronger correlations. **B.** The robustness, $\mathcal{R}$, of each interaction mode (Eq. 9) as a function of predator capture success probability, ω. Bins show the fraction of 10^6 random communities described by Eq. 5 that result in apparent competition (red), parasitism (blue), or mutualism (green) as predator capture probability, ω, is systematically varied. Parameter definitions and ranges for random communities are defined in Table 1; η is the relative carying capacity and reward potential of species 2, ω is the predator's capture probability, α_k are predator attack rates on prey k, χ_k are foraging resumption rates for prey k, and ρ_k are prey intrinsic growth rates. **C.** Empirical predator capture probabilities from $N = 8$ previously published laboratory and field studies (35 experimental animal groups in total). Pink lines show the median = 0.20 ($\pm$ 1 standard error measurement) capture success. Data sources provided in Robustness of apparent mutualism.

apparent mutualisms (Fig. 3A, note x-axis scale), we further analyzed the robustness, $\mathcal{R}$ (Eq. 9), of apparent mutualisms as capture success is systematically altered while all other parameters are drawn from random uniform distributions (Table 1; Fig. 3B). This metric estimates the probability that a random stable community will result in apparent competition, parasitism, or mutualism as ω varies. At low ω values, the system predominantly exhibits mutualism, while higher ω values shift interactions towards competition (Fig. 3B). Intermediate ω values display a mix of modes, including parasitism, indicating that predator capture probability is the most important parameter for determining interaction mode prevalence. Data on capture success probabilities for predatory animals are limited. However, 35 empirical estimates across 8 studies of flying and swimming predators (Sweatman 1984; Moyer 1987; Norton 1991; Hirvonen & Ranta 1996; Sancho 2000; Cresswell & Quinn 2010; Corcoran & Conner 2016; Thiebault *et al.* 2016) indicate that capture probabilities are commonly within the range of values predicted by our model to lead to positive indirect interactions (median capture success of 0.2; Fig. 3C).

Discussion

Behavioral plasticity in animals can significantly reshape species interactions, introducing new feedbacks that influence the structure and dynamics of ecological

networks (Neutel *et al.* 2007). Our study illustrates how such plasticity can alter not just direct interactions, but also the nature of indirect interactions, like those observed in classical apparent competition (Holt 1977) among prey. By integrating time scale separation from dynamical systems theory (Holling 1959; Segel & Slemrod 1989; O'Dwyer 2018; Strogatz 2018), we demonstrated that prey hiding behaviors can weaken or even invert these indirect effects, transforming negative interactions into positive ones under specific conditions. These findings align with earlier studies on shelter seeking (Sih 1987) and spatially explicit patch refuge models (Křivan 1998), which suggest that such behaviors generally promote species coexistence. Our study extends this understanding by demonstrating its role in controlling shifts in interaction *valence* — the qualitative nature of species interactions — based on conditions within the ecological network. In the case of hiding behaviors, we find surprising scenarios where persistent mutualisms, parasitism, and even neutrality can occur among apparent competitors (Fig. 2), and predator biomass increases with reduced hunting efficiency.

The population-level benefit of lower hunting efficiency in our model presents an intriguing area for further research (Abrams 1989). While efficient predators with high capture probabilities are known (Fig. 3C; Spencer *et al.* 2016), many predator-prey systems, especially those involving active pursuit and escape (Martin *et al.* 2022), exhibit low capture success rates. Empirical data from taxa including fish, birds, dragonflies, bats, and amphibians indicate that prey capture probabilities in the range of 0.01 to 0.2 are widespread (Moyer 1987; Sancho 2000; Sweatman 1984; Parrish 1993), with some more efficient predators achieving success rates around 0.4 (Cresswell & Quinn 2010; Corcoran & Conner 2016; Cresswell, Lind, *et al.* 2010; Thiebault *et al.* 2016; Hirvonen & Ranta 1996; Norton 1991) (Fig. 3C). These real-world capture success rates fall within the range predicted by our model for the emergence of positive interactions among prey. Documenting phenomena like apparent mutualisms in the field will likely be challenging however, requiring interaction time series data from individual wild animals. This level of data collection could be achieved with machine vision observatories (M. A. Gil & Hein 2017; Fahimipour, M. A. Gil, *et al.* 2023), drone technologies (Koger *et al.* 2023), or other continuous monitoring solutions (Davies & Asner 2014) to quantify both successful and failed interaction attempts in wild animal communities.

Our approach can be readily extended to other behaviors or behaviorally mediated interactions, allowing for the incorporation of additional forms of organismal plasticity into population dynamics models. Inspired by classical coarse-grained models like reaction kinetics from chemistry (Michaelis, Menten, *et al.* 1913) and the functional response from ecology (Holling 1959), we start by constructing a full system that includes subdivided populations that represent discrete behavioral or functional states in one or more species (Fig. 1). Assuming encounters between individuals are governed by mass-action laws can help formulate initial models when specific details on the transitions between states are unknown. A reduced model can then be derived by assuming a time scale separation — solving for the fast variables, considering these auxiliary variables, and substituting them back into the slow manifold (Keener & Keizer 2002; O'Dwyer 2018; Holling

1959; Hein & Martin 2020; Muscarella & O'Dwyer 2020). The power of this, and other, coarse-graining methods is that they can provide rapid analytical insights into which individual-level organismal behaviors might (or might not) influence dynamics at the scale of the entire ecosystem, or even when different microscopic animal behaviors map to the same macroscopic description of system dynamics (Wolpert *et al.* 2014; O'Dwyer 2018; D'Andrea *et al.* 2020).

While coarse-graining and time scale separation offer effective means to simplify complex systems, our findings reveal something perhaps more critical: routine animal behaviors can generate indirect effects that defy intuition — such as predators benefiting from higher failure rates due to interactions within their network motif, or competitors transitioning into mutualists. These results show how even small behavioral changes can spread through ecological networks, leading to unexpected cascading effects that reshape community structure and function. Understanding nontrivial relationships between scales is crucial for predicting and managing ecosystem resilience in a changing world, and may open the way for targeted interventions that modify specific organismal behaviors with broad impacts on ecological networks.

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